

BARU DARROWI GEN. ET SP. NOV., A LARGE, BROAD-SNOUTED
CROCODYLINE (EUSUCHIA: CROCODYLIDAE) FROM MID-TERTIARY
FRESHWATER LIMESTONES IN NORTHERN AUSTRALIA

PAUL WILLIS, PETER MURRAY AND DIRK MEGIRIAN

Willis, P., Murray, P. and Megirian, D. 1990 09 20: *Baru darrowi* gen. et sp. nov., a large, broad-snouted crocodyline (Eusuchia: Crocodylidae) from mid-Tertiary freshwater limestones in Northern Australia. *Memoirs of the Queensland Museum* 29(2): 521-540. Brisbane. ISSN 0079-8835.

Baru darrowi gen. et sp. nov., is a common element in limestones of late Oligocene to late Miocene age on Riversleigh Station in northwestern Queensland and at Bullock Creek in the Northern Territory. Although *Baru* is a member of the Crocodylinae and appears to have many features in common with certain early Tertiary crocodiles such as the North American *Brachyuranochampsia eversolei* Zangerl, it also resembles sebecosuchian and pristichampsine crocodiles in having ziphodont (serrated, laterally compressed) teeth similar to those of flesh-eating dinosaurs. The Australian ziphodont crocodile *Quinkana fortirostrum* Molnar, was previously considered to be closely related to the Pristichampsinae on the basis of its cranial profile and highly developed ziphodonty. *Quinkana fortirostrum* and *Baru darrowi* share characters not present in pristichampsine crocodiles and they appear to be more closely related to one another than to any other ziphodont taxa. Because *Baru darrowi* is clearly a member of the Crocodylinae, we propose that *Quinkana* and *Baru* represent a new crocodyline ziphodont clade and that these two forms, together with *Pallimnarchus pollens*, form a monophyletic endemic Australian radiation. □
Crocodylidae, Eusuchia, systematics, Tertiary, Ziphodont, Baru.

Paul Willis, University of New South Wales, GPO Box 1, Kensington, New South Wales 2033, Australia; Peter Murray and Dirk Megirian, Northern Territory Museum of Arts and Sciences, GPO Box 4646, Darwin, Northern Territory 0801, Australia; 22 August, 1990.

An unusually complete assemblage of fossil crocodile material has been recovered from fluvio-lacustrine sediments of middle to late Miocene age at Bullock Creek in the Northern Territory and late Oligocene to early Miocene age on Riversleigh Station, Queensland. The material provides clear evidence of a member of the subfamily Crocodylinae possessing ziphodont teeth. Previous finds of Australian ziphodont crocodiles have not been complete enough to determine their subfamilial affinity with confidence (Hecht and Archer, 1977; Molnar, 1981, 1982). The material described here is referred to the new genus and species *Baru darrowi*, a large crocodilian with many distinctive features. Its broad, short snout, robust proportions and deeply festooned jaws set it apart from any living *Crocodylus* species. Its dentition consists of posteriorly inclined, slightly recurved, laterally compressed crowns of greatly varying dimensions, bearing well-developed anterior and posterior crests (carinae). In some Northern Territory specimens, these carinae are finely serrated like the teeth of South American

sebecosuchian and Northern Hemisphere early Tertiary pristichampsine crocodiles. Oddly, no specimens of *Baru* from the Riversleigh deposits have serrated carinae. Large, slightly compressed carinate teeth with fine serrations are also known from the Alcoota Local Fauna of the Northern Territory (P.M., pers. obs.) and from other middle to late Tertiary localities throughout the interior of Australia. These have been variously assigned to the genus *Pallimnarchus* (Molnar, 1982) or to unidentified sebecosuchians (Hecht and Archer, 1977). It can now be demonstrated that at least some of the ziphodont crocodile teeth found in Australia belong to a crocodyline genus. The proposition that pristichampsine and sebecosuchian ziphodont crocodiles may have been present in Australia is therefore re-examined.

Quinkana fortirostrum (Molnar, 1981), the first Australian crocodile formally described as a ziphodont, is known primarily from a snout. Although sufficiently well represented to suggest a closer affinity with *Baru darrowi* than with *Pristichampsus*, its principle features are

dominated by trophic specialisations. Because crocodylians are otherwise structurally conservative, there are few character states suitable for a cladistic evaluation. We are therefore confined to a few observations strongly supporting the more parsimonious hypothesis that Australian ziphodont crocodiles represent a monophyletic radiation with Gondwana as its likely origin.

Interpretation of the polarity of character states, and basic concepts of crocodylian phylogeny used in this study, are based on Molnar (1981), Benton and Clark (1988) and Langston (1973); nomenclature follows Steel (1973) and Iordansky (1973). Prefixes used to indicate the source of specimens are as follows: NTM P, Northern Territory Museum, Palaeontological Collections; NTM R, Northern Territory Museum, Reptile Collections; QM F, Queensland Museum, Fossil Collections; SAM P, South Australian Museum, Palaeontological Collections.

Order CROCODYLIA Gmelin, 1700
Suborder EUSUCHIA Huxley, 1875
Family CROCODYLIDAE Cuvier, 1807
Subfamily CROCODYLINAE Cuvier, 1807

***Baru darrowi* gen. et sp. nov.**

GENOTYPIC SPECIES

Baru darrowi sp. nov. (Fig. 1a-c).

DIAGNOSIS

Species of *Baru* differ from all other crocodylines in the following combination of features; Broad moderately deep snout containing thirteen maxillary teeth; five premaxillary teeth present in juveniles and four in adults owing to loss of the second tooth; premaxillary and anterior six maxillary teeth directed posteriorly; tooth crowns moderately compressed bucco-lingually with carinae on the anterior and posterior margins; tooth crown and socket dimensions highly differentiated along both upper and lower tooth rows with correspondingly wide, deep alveolar processes; conspicuous maxillary reception pits, corresponding to dentary tooth crowns, situated lingual to the upper tooth row; anterior margin of the palatal fenestrae extending to the level of the seventh maxillary tooth; anterior palatine process absent; mandibular symphysis extends posteriorly to between the sixth and seventh dentary teeth; splenial terminates anteriorly at the level of the seventh dentary tooth and does

not enter symphysis; internal nares with raised rim; external nares terminal; distinctive bony crest arches posteriorly from the maxillae and jugals, extending to the quadratojugals.

ETYMOLOGY

'Baru' is the Dreamtime Crocodile Man from the Aboriginal mythological lore of Eastern Arnhem Land (Groger-Wurm, 1973). The specific name honours British actor Paul Darrow, best known for his role in the television series 'Blake's Seven', in recognition of his support of continuing palaeontological investigations of the Riversleigh deposits.

SPECIFIC DIAGNOSIS

That of the genus until additional species are known.

MATERIAL EXAMINED

HOLOTYPE. NTM P8695-8, a nearly complete cranium missing the skull roof (frontals, parietals, postorbitals and squamosals) and basicranium posterior to the orbits.

PARATYPES. From D-Site, Riversleigh: NTM P8778- (1-5), right posterior mandible fragment, right posterior skull fragment preserving the lateral temporal fenestra, right pterygoid, ectopterygoid and posterior region of the maxilla; NTM P8681-14, left mandible lacking the articular and adjacent angular and surangular posterior to the lateral foramen and a small portion of the dentary at the level of the third tooth; NTM P8738-1, right jugal, pterygoid, ectopterygoid and posterior maxilla and an associated dentary fragment; QM F16822, premaxilla and anterior portion of left maxilla retaining fourteen teeth; from Pancake Site, Riversleigh: SAM P27866, right premaxilla; from Blast Site, Bullock Creek, NTM P87103-11, left squamosal, quadrate and opisthotic (juvenile).

REFERRED SPECIMENS. From D-Site, Riversleigh: QM F16823, jugal fragment; QM F16824, premaxillary fragments; QM F16825, right dentary; QM F16826, right dentary; From Site Y, Bullock Creek, NTM P87105-1, right mandible fragments, From Blast Site, Bullock Creek, NTM P87103-12, juvenile right maxilla; NTM P8697-2, right jugal.

TYPE LOCALITY.

Blast Site, Camfield Beds, located '16 miles southeast of Camfield Homestead in north central Northern Territory' (Plane and Gatchouse, 1968).

AGE

Late Oligocene to mid Miocene.

TABLE 1. Snout proportions of *Baru* and other crocodilians.

Taxon	H/L	H/W	W/L
<i>Brachyuranochampsia eversolei</i>	—	—	0.40
<i>Sebecus icaeorhinus</i>	0.39	1.37	0.28
<i>Pristichampsus vorax</i>	0.24	0.51	0.48
<i>Quinkana fortirostrum</i>	0.36	0.51	0.70
<i>Osteolaemus tetraspis tetraspis</i>	0.35	0.35	1.00
<i>Osteolaemus tetraspis osborni</i>	0.31	0.41	0.74
<i>Paleosuchus palpebrosus</i>	0.29	0.48	0.60
<i>Crocodylus porosus</i>	0.21	0.37	0.57
<i>Alligator mississippiensis</i>	0.26	0.28	0.93
<i>Gavialis gangeticus</i>	0.09	0.54	0.16
<i>Baru darrowi</i>	0.68	0.94	0.72

L is the distance from the anterior extremity of the orbit to the posterior extremity of the external nares, H is the maximum depth of the snout at the fifth alveolus, and W is the maximum breadth of the snout at the fifth alveolus. Values for the first seven taxa are from Molnar (1981, p. 809). Values for *Crocodylus*, *Alligator* and *Gavialis* are from Australian Museum Specimens (AM R32646, AM R130772 and AM R131340 respectively). Values for *Baru* are from NTM P8695-8.

STRATIGRAPHY

Vertebrate thanatocoenoses often occur as geographically or stratigraphically discrete assemblages in the middle Tertiary limestones of northern Australia. Because of uncertainty about the relationships (temporal and ecological) of these assemblages, it has become common practice to treat each as a separate local fauna (sensu Tedford, 1970).

Archer et al. (1989) suggest three significant time periods are represented at Riversleigh between the Oligocene and the Miocene. Woodburne et al. (1985) suggest a mid to late Miocene age for the Bullock Creek Local Fauna. However, if the more derived Alcoota Local Fauna is also considered late Miocene, the Bullock Creek Local Fauna is more appropriately designated as mid Miocene.

The specimens of *Baru darrowi* from Bullock Creek were collected from the Blast Site and nearby Site Y, approximately 17°S, 131°30'E. It is not yet clear that any particular Bullock Creek site assemblage is significantly different from any other and all have been tentatively referred to the Bullock Creek Local Fauna (Murray et al., in prep.).

Consequently, the age range of *Baru darrowi* probably extends from late Oligocene (Riversleigh) to mid Miocene (Bullock Creek).

DESCRIPTION

Because of the limited comparative material available, *Baru darrowi* is compared with the living saltwater crocodile, *Crocodylus porosus*. However, *Baru* has much in common with more archaic crocodylines (e.g. a wide incisive foramen and overlapping bite (Langston, 1973)), conditions apparently lost among the more derived living genera. Large triangular palatal fenestrae were also characteristic of many early Tertiary crocodylines. A comparison of the snout proportions of *Baru darrowi* with other crocodilians is given in Table 1. Table 2 provides a classification of snout proportions according to Molnar (1981). Table 3 lists specific features of *Baru darrowi* and compares them with other crocodilians.

Cranium. The cranium of *Baru darrowi* is triangular in dorsal profile and trapezoidal in section at the level of the maxillo-jugal suture. Compared to *C. porosus* the cranium of *Baru* is much deeper and broader in proportion to its length (Table 1). In lateral profile (Fig. 1A) the cranium is deep, slightly wedge-shaped and nearly as high immediately posterior to the narial aperture as it is just anterior to the orbits. The dorsal outline of the snout is concave. The profile of the premaxilla is distinctive in its shortness and depth. The anterior margin is a vertical surface, rounded ventrally and demarcated posteriorly by a wide notch for the caniniform fourth mandibular tooth. In dorsal view (Fig. 1B) the premaxillae describe a broad, D-shaped surface immediately anterior to the tooth notches. Posterior to the constriction, the maxillae widen over laterally swollen alveolar festoons. Posteriorly the maxillae become more steep sided, slab-like and shallowly concave. Dorsally the nasomaxillary junction is accentuated by a low crest. The alveolar process (sensu Molnar, 1981) is a wall of interconnected, buttressed alveoli. Anteriorly the alveolar process is strongly festooned but posteriorly it is more uniform.

The jugal extends deeper ventrally and the maxillo-jugal suture is longer than in *C. porosus* of comparable size. The subtemporal ramus of the jugal widens laterally. Lateral to the lateral temporal fenestra this process is dorsoventrally flattened gradually becoming more rounded in cross section lateral to the quadratojugal. The lateral edge of the subtemporal ramus extends anteriorly as a ridge onto the broad anterior face of the jugal. In lateral view, the shape and size of the orbit is similar to and no less dorsally situated than in *C. porosus*. A well preserved

TABLE 2. Classification of snout proportions.

A. SNOUT DEPTH (H/W)		B. SNOUT BREADTH (W/L)*	
Low	$x < 0.5$	Broad	$x \geq 0.66$
Moderately deep,	$0.5 \leq x < 1.0$	Moderately Narrow	$0.66 > x > 0.33$
Deep	$x \geq 1.0$	Narrow	$x \leq 0.33$

* Molnar (1981,p.817) states that this ratio is L/W. This contradicts discussion of snout width ratios elsewhere in that paper. Molnar (pers. comm.) reveals that this ratio was intended to be W/L (not L/W). Classification of values for snout depth and snout breadth ratios according to Molnar (1981,p.817).

portion of the jugal and quadratojugal indicates that the lateral temporal fenestra was both longer and wider than in any living crocodyline species.

In dorsal aspect, the posterior of the cranium is about one-third broader than a *C. porosus* of equivalent length and the anterior is broader by a quarter. The premaxillae are wider relative to their length than in the Saltwater Crocodile and the narial aperture is shorter and broader. It extends to the anterior margin of the premaxillae. Reception sockets for the first dentary teeth do not breach the outer surface of the snout as in *C. porosus*.

Sutural relations on the dorsal surface of the cranium are essentially like those of *C. porosus* (Fig. 2). Well-developed dorsal processes of the premaxillae project posteriorly alongside the nasals. The premaxillae join in the midline anterior to the nasals, excluding them from the external nares. The paired nasals are elliptical in shape and slightly expanded posteriorly, shorter and less wedge-like than in *C. porosus*. The maxillae are greatly expanded laterally into deep, steep-sided lobes, which flatten out posteriorly before expanding outwards again at the base of the jugals.

In the large mature specimen, the sutural pattern of the upper facial region is partly obscured by age-related fusion and elaborate bony ornamentation. The basic pattern is like that of *Crocodylus* spp. The lachrymal extends anteriorly to meet the nasal bone, so excluding the prefrontal from contacting the maxilla. The prefrontal forms the anteromedial orbital margin. The posteromedial half of the orbit is formed by the orbital process of the frontal (Fig. 2). The position of the orbits, their shape and the morphology of the interorbital area are essentially the same as in *C. porosus*. The shape of the orbits of *Baru* differ from those of *C. porosus* only in being slightly longer, wider posteriorly and also more pointed anteriorly (Fig. 1B). The quadratojugals and jugals form a wide shelf bounding the comparatively large, triangular lateral tem-

poral fenestra (approximately 52.0mm wide by 86.0mm long in NTM P8778-4). This opening is about twice the length of that of a *C. porosus* of equivalent size. A portion of the superior temporal fenestra is also preserved on that fragment and on a fragment of the skull roof of a much smaller individual, NTM P87103-11. These indicate that the proportions of the superior temporal fenestrae were similar to those of *C. porosus*. The auditory meatus is more anteriorly placed in *Baru* than it is in *C. porosus*. The portion of squamosal preserved on NTM P87103-11 indicates that the skull roof of *Baru* was flat and wider posteriorly than in *C. porosus*.

The ventral surface of the cranium is dominated by the broad, flat maxillary palate with its wide alveolar processes and by the large triangular, anteriorly located palatal fenestrae (Fig. 1C). The premaxillae are penetrated by a large, oval incisive foramen recessed within a deep fossa, the anterior portion of which is confluent with a pair of reception pits for the first dentary teeth. In combination with the wide, deep alveolar process containing four large tooth sockets on each side, the premaxillary palate is distinctly vaulted in contrast to the relatively flat premaxillary palate of *C. porosus*. The maxillary palate is broad and short and is elevated above the alveolar margins. A row of small nutrient foramina clearly define the maxillary palate. The maxillary alveolar process is greatly expanded to accommodate the enlarged fourth and fifth maxillary caniniform teeth. Like *Caiman* and *Ossteolaemus*, *Baru darrowi* has fewer maxillary teeth than *C. porosus* and the size range of the tooth sockets and their corresponding teeth is greater than in any living crocodile. *Baru* specimens have a consistent number of thirteen maxillary teeth, as in the broad-snouted caimans. The moderate lateral compression of the tooth crowns of *Baru* is not clearly reflected in the shape of the alveoli which are predominantly round (Figs 1C,2,5A). The anterior maxillary teeth are posteriorly directed. The genus also

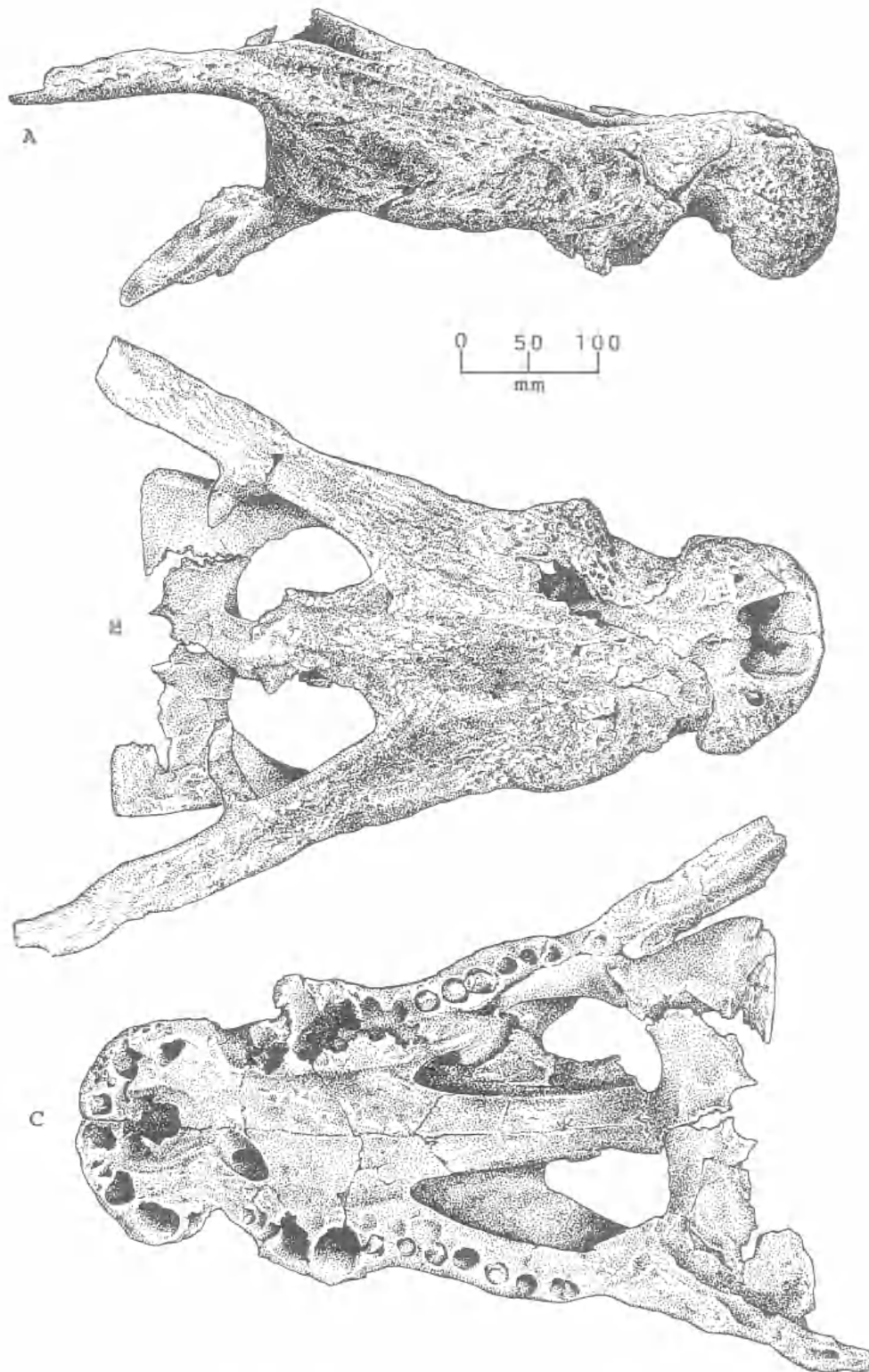


FIG. 1. *Baru darrowi* holotype, NTM P8695-8: (A) lateral view; (B) dorsal view; (C) ventral view.

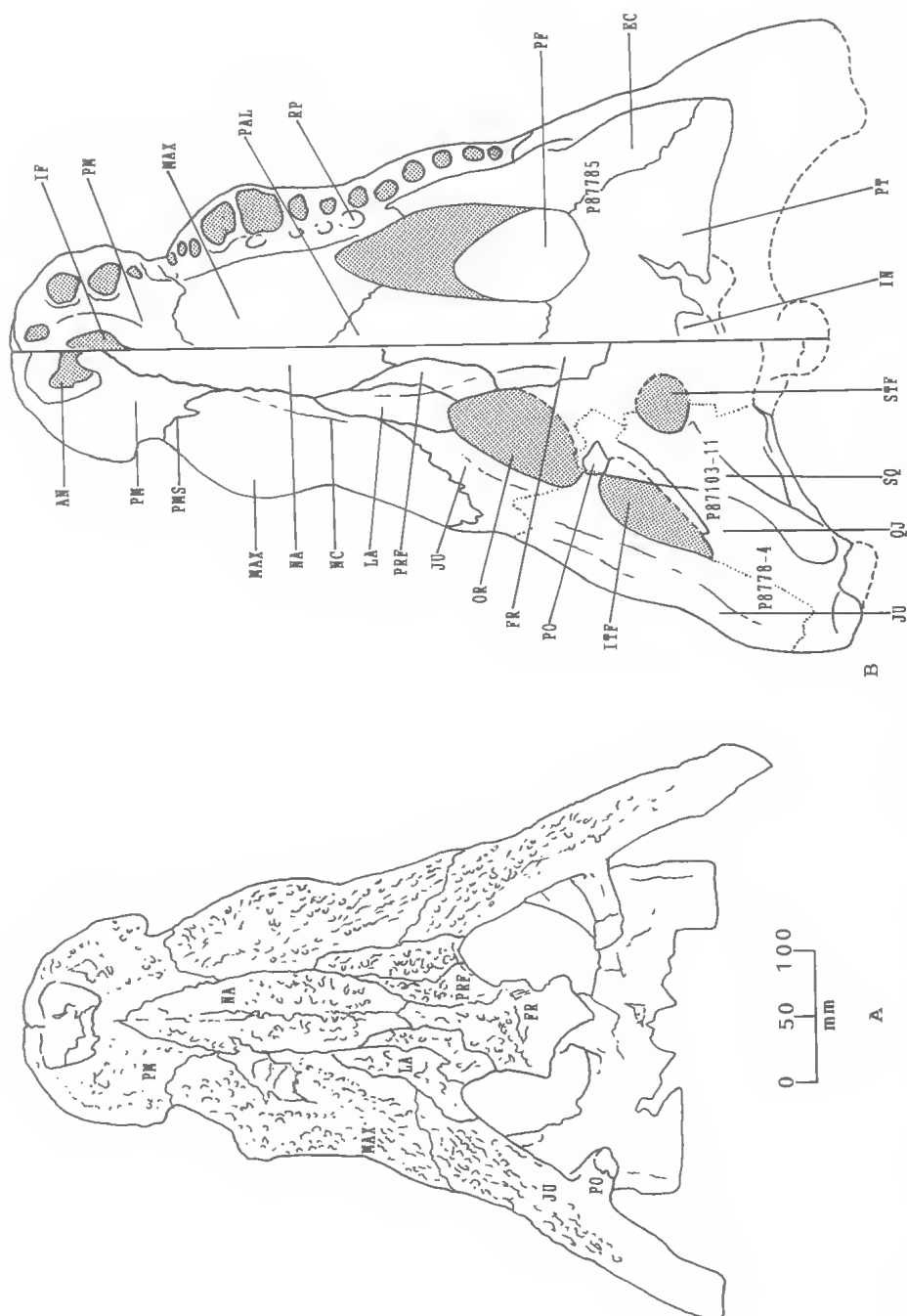


FIG. 2. (A) Interpretation of the dorsal sutures of the *Baru darrowi* holotype, NTM P8695-8. In this specimen many of the dorsal sutures are partially obscured by age obliteration and ornamentation. (B) Composite restoration, dorsal and ventral views, of *Baru darrowi* showing structures. Catalogue numbers (all with NTM prefix) indicate portions of the skull not represented, or poorly represented, on the holotype NTM P8695-8. Abbreviations: AN, anterior naris; NC, nasal crest; OR, orbit; PAL, palatine; PF, palatine foramen; IN, internal naris; ITF, lateral temporal fenestra; JU, jugal; LA, lacrimal; MAX, maxilla; NA, nasal; PM, premaxilla; PMS, premaxillary suture; PO, postorbital; PRF, prefrontal; PT, pterygoid; QJ, quadrate; SQ, squamosal; STF, superior temporal fenestra.

differs from *Crocodylus* in that the crowns of the lower dentition occlude inside the upper tooth row, the longer dentary teeth having reception pits between and mesial to maxillary teeth four through eight.

The palatal fenestrae of *Baru darrowi*, in addition to their large size and distinctive shape, invade the maxillary palate anteriorly to the level of the seventh maxillary tooth (Figs 1C, 2B). In *C. porosus* the fenestrae extend only to the ninth maxillary tooth. In this respect also, *Baru* is similar to short-faced crocodyline *Osteolemus tetraspis* and the equally short-faced alligatorine, *Paleosuchus trigonatus*. It differs from all living and most extinct crocodylids in lacking anterior palatine processes. The course of the maxillo-palatine is a wide chevron between the anteromedial margins of the palatal fenestrae. The palatine bones are concave medially to accommodate the long, posteriorly wide palatal fenestrae. In contrast to *C. porosus* but like *C. novae-guineae*, the posterior margins of the palatal fenestrae are formed mainly by the pterygoids.

In keeping with the width of the back of the cranium, the pterygoids are broad. In lateral profile, the ectopterygoids are longer and project ventrally at a somewhat different angle than in *C. porosus*. The posteroventral process of the ectopterygoids appears to be slightly longer than that of *C. porosus* and the anterior (palatal) process is decidedly more robust. Overall dimensions of the holotype are given in Figs 3A-C.

Mandible. NTM P8681-14 comprises an almost complete left mandible lacking only surangular posterior to the external fenestra, the coronoid, and a short length of the dentary bearing the third tooth. The first, second, fourth, fifth, sixth, fourteenth and fifteenth teeth are preserved. In general proportions the mandible is slightly larger than that of an approximately four-metre-long *C. porosus* (NTM R13748). In occlusal view (Fig. 4a) the symphysis extends posteriorly to just beyond the level of the sixth tooth. In *C. porosus* it ends level with the fifth tooth. The angle between the axis of the mandibular ramus and the symphyseal plane is similar to that of *C. porosus*. The lateral surface of the mandible and the tooth row are concave laterally in contrast to a gentle convexity in *C. porosus* (Fig. 4a). The caniniform fourth tooth and its broad alveolus protrude laterally. NTM P8681-14 shows a slightly greater variation in alveolar size than *C. porosus* although the pattern of tooth differentiation is basically the same.

A pronounced difference in alveolus shape is exhibited by the confluence of the tenth and eleventh, whereas in *C. porosus* the alveoli are usually separated by between five and ten millimetres of bone.

The greater degree of festooning in *Baru* reflects the enlargement of the caniniform fourth tooth and the laterally compressed tenth and eleventh teeth. As in *C. porosus*, *Baru* has a conspicuous excavation on the lateral surface of the dentary to accommodate the upper fourth and fifth maxillary teeth (Fig. 4b).

The coronoid is not preserved on any specimen nor are there any examples of a complete Meckelian fossa. Incomplete specimens indicate that the Meckelian fossa was similar in size to *C. porosus*. In the Bullock Creek specimen NTM P87105-1, the long axis of the Meckelian fossa is aligned at a relatively high angle (c. 25°) to the inferior border of the mandibular ramus; in Riversleigh specimens and *C. porosus* it is nearly parallel to the inferior border (Figs. 4b, 5c).

The lateral mandibular ramus is more heavily sculptured than that of *C. porosus*. In NTM P8779-2 and NTM P87105-1, the sculptured region on the angular and surangular is delineated from the adjacent smooth bone by a prominent margin. In *C. porosus*, the two surface textures in this region grade into each other. The external mandibular fenestra is narrower dorsoventrally and the posterior upward inflection of the inferior border of the mandibular ramus is greater in *Baru darrowi* (Figs 4b, 5b-c). On NTM P8681-14, a 5.0mm wide longitudinal sulcus originates from a small foramen located about 45.0mm from the last tooth. A similar sulcus is not evident on any *Crocodylus* specimens in our possession. A damaged articular is preserved on NTM P8778-2 (Fig. 4b). It has a somewhat longer anterior process entering the adductor fossa than that of *C. porosus*, thus providing a relatively larger sutural contact with the angular.

Sutural relations between the mandibular elements show only minor differences from those of *C. porosus*. In NTM P87105-1 and NTM P8778-2 the angular and surangular butt against each other within the adductor fossa and terminate anteriorly high on the posteroventral margin of the external fenestra. In *C. porosus* they meet at a lap joint and the suture contacts the external fenestra in the mid-region of the posteroventral border.

VARIABILITY

On the basis of a limited selection of material,

Baru darrowi has been described as a variable species that existed over a considerable span of geological time. The possibility that more than one *Baru* species was present between Riversleigh and Bullock Creek times has been considered. At present, there is insufficient evidence to support a specific separation of the two populations due to lack of information about sexual dimorphism, ontogenetic changes and allometry in these extinct crocodiles. By analogy with living crocodiles, at least some observed differences between the Riversleigh and Bullock Creek specimens could be attributed to these factors.

One of the more intriguing differences between the two populations is the absence of serrations on the carinae of the teeth in the Riversleigh *Baru* sample. Riversleigh *Baru* specimens also have a more pointed premaxilla when viewed from the dorsal aspect. This may also relate to the apparently longer span between the fourth and the first dentary teeth observed in Riversleigh mandibles. While attempting to reconstruct *Baru* for an illustration, one of us (P.M.) was unable to match the length of the Riversleigh symphysis to the Bullock Creek premaxilla, although the remainder of the mandible seemed to fit reasonably well in terms of size and shape. A single specimen of the dentary symphysis from Bullock Creek is proportionally shorter and fits the contours of the premaxilla of the holotype. Differences in the angle of the long axis of the mandibular fenestra to the inferior border of the mandibular ramus are noted above. Given the current state of resolution, we consider the definition of a single chronospecies subsuming these variations to be adequate for the time being.

COMPARISONS WITH OTHER CROCODYLIDS

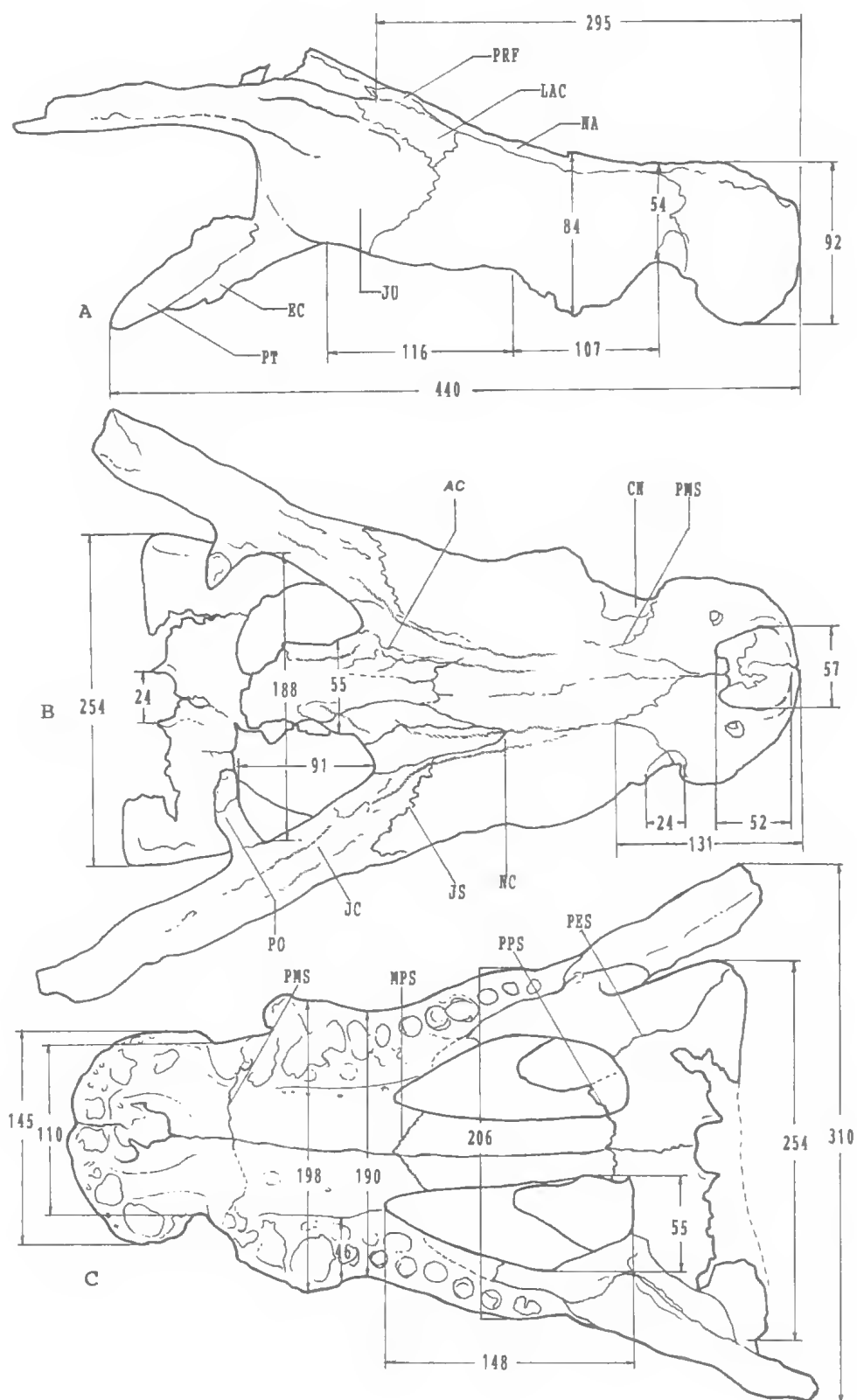
Wider comparison of *Baru darrowi* emphasises some of its more unusual features. This comparison is unavoidably brief and incomplete due to our limited comparative material. We confine our observations to crocodylians which

have certain obvious similarities to *B. darrowi* either in terms of the dentition or cranial morphology.

Living Crocodylids. Of living crocodylid species, *Baru darrowi* most closely resembles such broad-snouted forms as *Osteolaemus tetraspis* among the crocodylines and *Paleosuchus trigonatus* among the alligatorines (Table 1). Similarities include the number of maxillary teeth (13) and the size and position of the palatal fenestrae (Table 3). *Paleosuchus* spp. also possesses the alligatorine overbite which is similar to the condition in *B. darrowi*. Some caiman species have marked differences in tooth size, festooning and large caniniforms, whereas *Osteolaemus tetraspis* appears to have mildly durophagous specialisations. Although the palatal fenestrae of both forms are very large and end at the level of the seventh maxillary tooth, as in *B. darrowi*, they are differently shaped and have somewhat different proportional contributions to their margins from the surrounding palatal complex. A conspicuous difference is the presence in both living forms of a well defined anterior palatine process, absent in *B. darrowi*. These striking proportional similarities indicate that a substantial portion of *Baru*'s rostral morphology is trophically dedicated, derived and the result of parallel evolution. Similar remarkable parallel developments within various crocodylian lineages are discussed by Langston (1973).

The extent to which *B. darrowi*'s rostral proportions differ from *Crocodylus porosus* depends largely upon the state of maturity of the specimens compared. The holotype is obviously an adult and bears little resemblance to young specimens of *C. porosus*. However, when compared to a very large *C. porosus*, the width to length proportions (Webb and Messel, 1978) of *Baru* appear to differ very little (Fig. 6). This brings us to the peculiar case of the 'Lansdowne snout' (QM F1752), a Pliocene crocodile rostrum recovered from Lansdowne Station, Queensland. It was originally described as *Pallinarchus pollens* (Longman, 1925) but was

FIG. 3. (A) Lateral view of *Baru darrowi* holotype NTM P8695-8 showing structures and dimensions. All measurements in millimetres. Abbreviations: EC, ectopterygoid; JU, jugal; LAC, lachrymal; NA, nasal; PRF, prefrontal; PT, pterygoid. (B) Dorsal view of the *Baru darrowi* holotype NTM P8695-8 showing structures and dimensions. The two circular structures on the premaxilla are artefacts produced by the breaching of the dorsal surface by the alveoli of the upper teeth. All measurements in millimetres. Abbreviations: AC, antorbital crest; CN, canine notch; JS, jugal sulcus; JU, jugal; NC, nasal crest; PMS, premaxillo-maxillary suture; PO, postorbital. (C) Ventral view of the *Baru darrowi* holotype NTM P8695-8 showing structures and dimensions. Abbreviations: MPS, maxillo-palatine suture; PES, pterygoid-ectopterygoid suture; PMS, premaxillo-maxillary suture; PPS, palatine-ptyerygoid suture.



later assigned to *C. porosus* (Molnar, 1982). The Lansdowne snout is proportionally shorter and broader than that of the *B. darrowi* holotype. Its ventral profile, moreover, closely resembles that of *B. darrowi* in its exaggerated maxillary swellings, short, broad premaxillary outline, its overbite, and, so far as can be determined from

illustrations (viz Molnar, 1982; fig. 5), its large and anteriorly positioned palatal fenestrae. Work in preparation by one of us (P.W.) and Molnar suggests that the Lansdowne snout should be referred to *Pallimnarchus* after all, but perhaps not *P. pollens*.

Fossil Crocodylines. In addition to its short

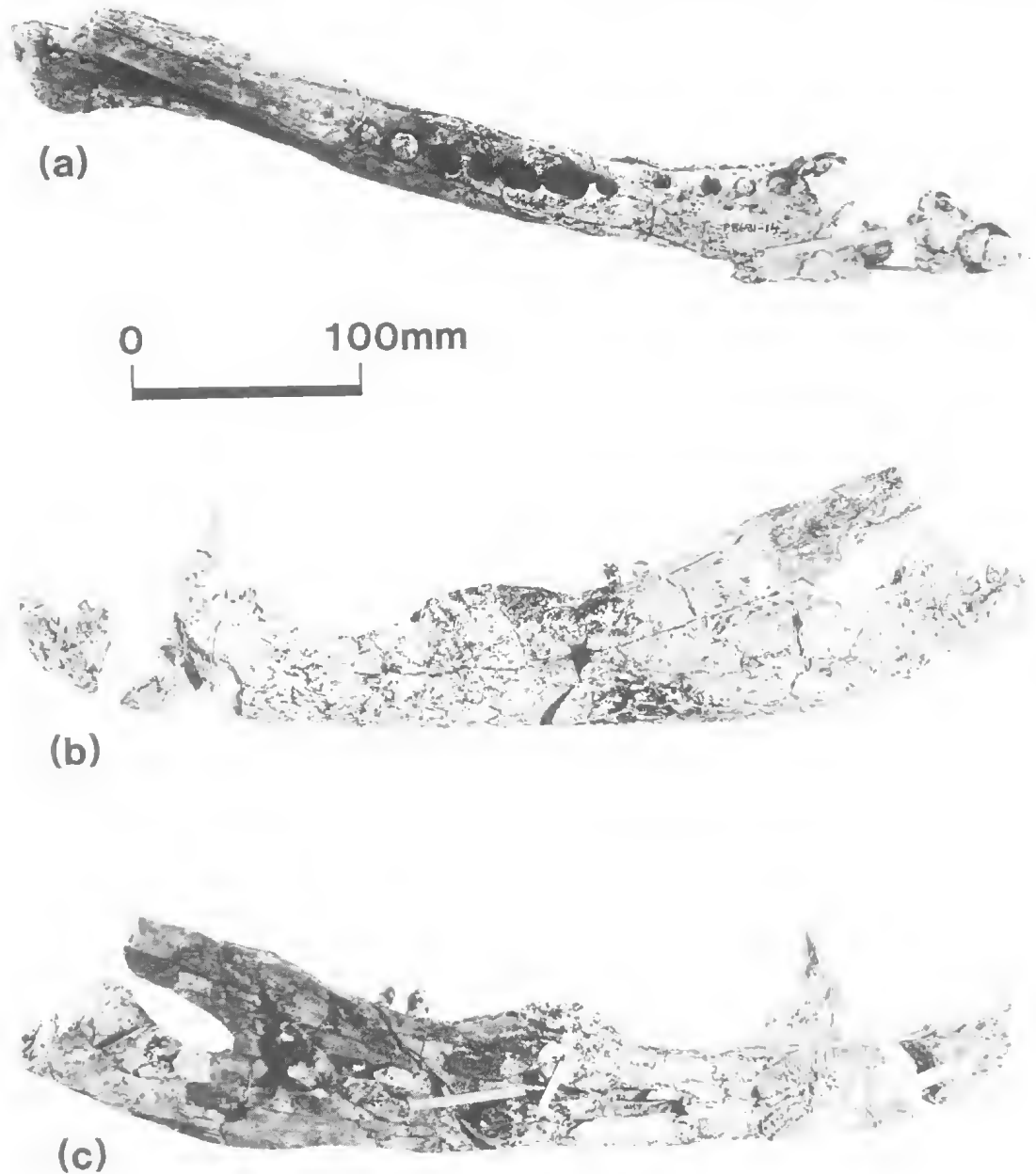


FIG. 4. *Baru darrowi*, NTM P8681-14, left mandible from 'D-Site', Riversleigh: (a) occlusal view; (b) lateral view; (c) medial view.

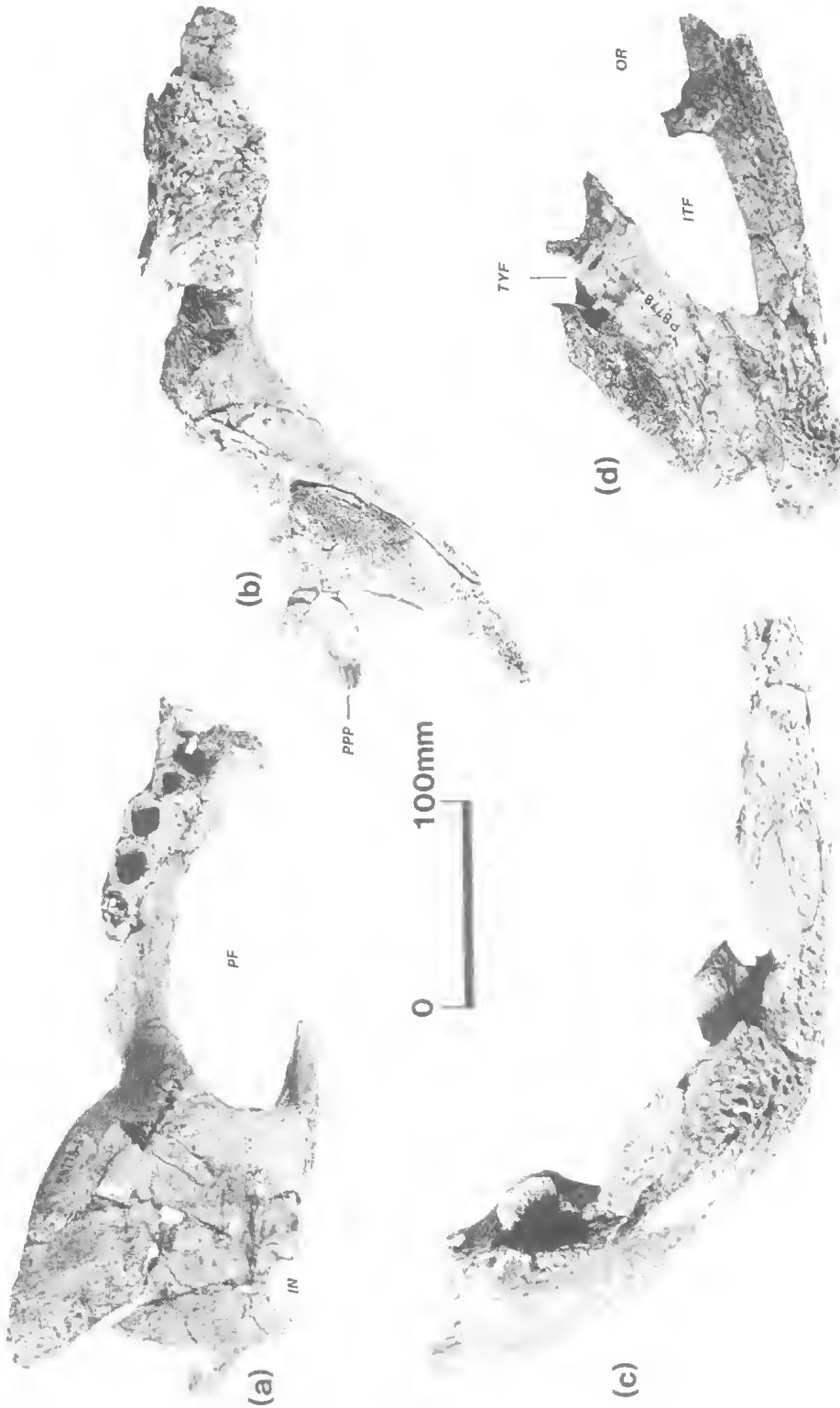


FIG. 5. *Baru darrowi*, NTM P8778 individual from 'D-Site', Riversleigh: (a) ventral view, NTM P8778-5, right pterygoid, ectopterygoid and posterior region of maxilla; (c) NTM P8778-2, right posterior mandibular fragment, lateral view; (d) NTM P8778-4, right posterolateral skull fragment, dorsal view. Abbreviations: IN, internal nares; ITF, lateral temporal fossa; OR, orbit; PF, palatine fenestra; PPP, posterior pterygoid process; TYF, tympanic fenestra.

TABLE 3. Characters of *Baru darrowi* and their distribution.

CHARACTER	A	B	C	D	E	F	G	H	I	J
1. Procoelous vertebrae	p	?	?p	a	p	p	p	p	p	p
2. Internal nares	Pt	?	?Pt	Pt/P	Pt	Pt	Pt	Pt	Pt	Pt
3. Tooth enlargement sequence	c	c	c	—	c	c	al	c	c	c
4. Tooth notch	p	p	p	p	p	p	a	p	p	p
5. Lacrymal/nasal contact	p	p	p	p	p	p	a	p	p	p
6. Palatal fenestrae position (Mx. tooth number)	7-8	7	7	10	10	9	12	7-8	7	8-9
7. Palatal process	a	a	a	p	p	p	p	a/p	a/p	a
8. Occlusion	o	o	o	o	o	i	o	o	i	o
9. Jugal ridge	a	p	p	?p	?p	p	p	?p	?p	?p
10. Pseudoheterodonty	p	a	p	a	a	p	p	p	p	p
11. Festooning	p	a	p	a	a	p	p	p	p	p
12. Snout width	b	b	?	n	m	b	b	b	b	m
13. Snout depth	md	md	?	d	md	l	l	md	l	?
14. Tooth compression	p	p	a	p	p	a	a	a	a	?
15. Serrated carinae	p	p	p	p	p	a	a	a	a	?
16. Teeth inclined to posterior	p	a	a	a	a	a	a	a	a	?

Key to species: A, *Baru darrowi*; B, *Quinkana fortirostrum*; C, *Pallimnarchus pollens*; D, *Sebecus icaeorhinus*; E, *Pristichampsus vorax*; F, *Crocodylus porosus*; G, *Alligator mississippiensis*; H, *Paleosuchus osborni*; I, *Osteolaemus tetraspis*; J, *Brachyuranochampsia eversolei*. Key to character states: a, absent; al, alligatorine; b, broad; c, crocodyline; d, deep; i, interlocking; l, low; m, moderately narrow; md, moderately deep; n, narrow; o, overbite; p, present; Pt, pterygoid only; Pt/P, palatine and pterygoid contact. Interpretations from the following sources: A, B, C, F and G from specimens; D from Colbert (1946); E from Langston (1975); H and I from Mook (1921); J from Zangerl (1944); all interpretations were compared and completed from Molnar (1981).

snout, *Baru darrowi* has a distinctive broadly triangular cranium, great width of the jugals lateral to the orbits, elongation of the inferior temporal fenestra, large triangular palatal fenestrae that constrict the palatines posteriorly, absence of the anterior palatine processes and the elliptical shape of the nasal bones.

Crocodylines with similar features were widespread in North America in the early Tertiary. One of the best preserved of these crocodylines is *Brachyuranochampsia eversolei* Zangerl, 1944, from the Washakie Eocene of Wyoming, U.S.A. Like *Baru*, *Brachyuranochampsia* combines the presence of a crocodyline notch for the fourth dentary tooth with an alligatorine-like overbite denoted by a series of reception pits medial to the upper tooth row. Although *Brachyuranochampsia* is a moderately narrow-snouted crocodyline (Table 1) it is heterodont and the alveoli are closely approximated. The jugals are broad and everted, nasals are elliptical, inferior temporal fenestra are large, the quadrates and quadratojugals are broad. The nasal aperture, although damaged anteriorly appears to have been terminal or near-

ly so and trapezoidal in shape, like that of *Baru*, in contrast to the elliptical nares of *Crocodylus* spp. The palatal structure resembles *Baru* in its lack of an anterior palatine process and large, triangular palatal fenestrae and palatines that narrow posteriorly rather than widen as in *Crocodylus*. However, unlike *Baru* its dentition is not ziphodont and fourteen rather than thirteen maxillary teeth are present. The palatal fenestrae extend anteriorly only to a level between the eighth and ninth maxillary teeth. This is consistent with the observation that short-snouted crocodylines have more anteriorly-positioned palatal fenestrae. With our present state of knowledge it would be imprudent to force *Baru* into a phyletic relationship with this particular American genus, which may be expressing a symplesiomorphic character complex widely distributed among primitive early Tertiary crocodylines. However, given the dearth of other living and fossil forms that lack the anterior palatine processes combined with the broad similarities previously mentioned, the likelihood of an entirely parallel development of these features seems fairly remote.

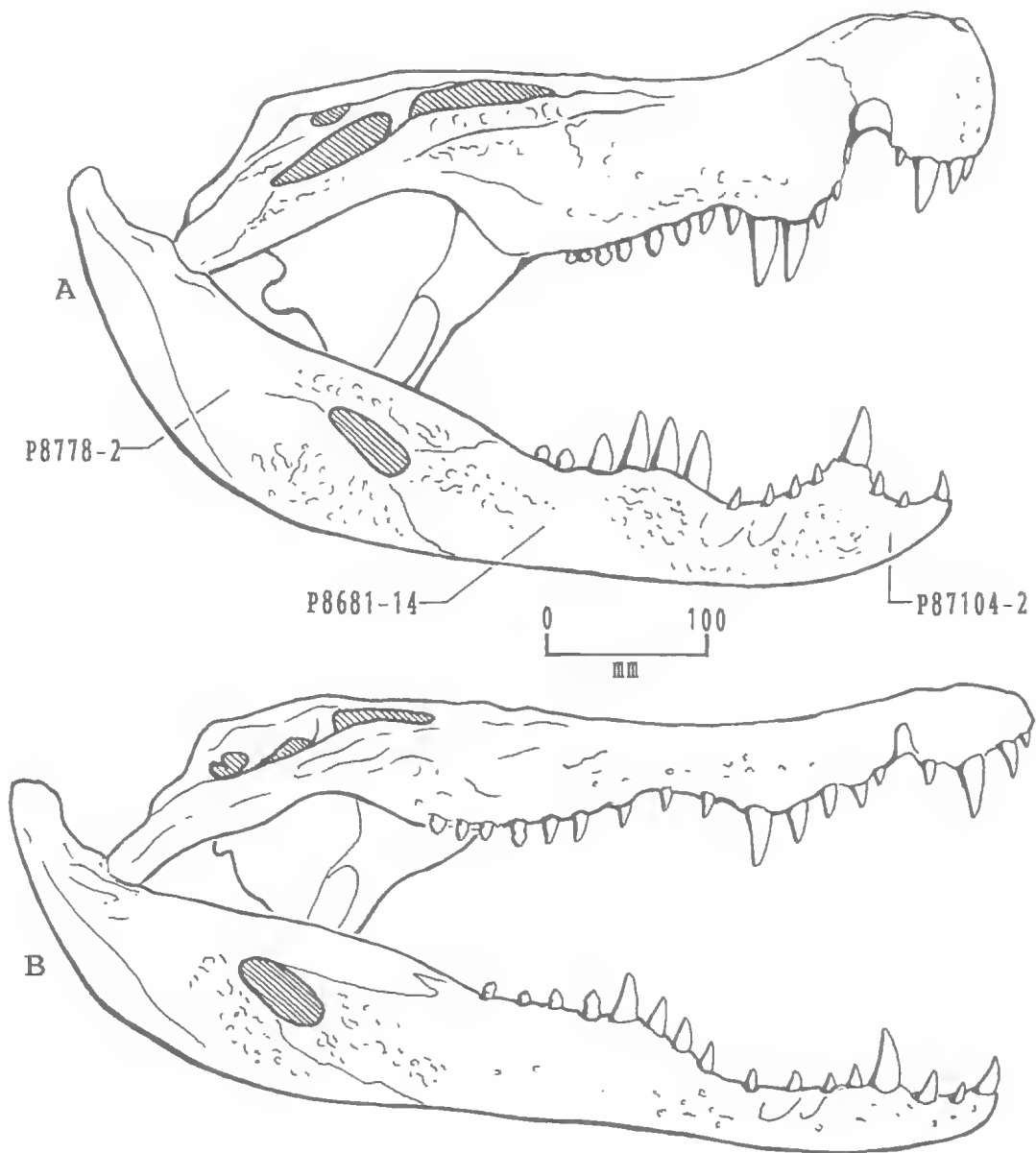


FIG. 6. Comparison of the lateral profiles of the skulls of (A) *Baru darrowi* and (B) an extant saltwater crocodile, *Crocodylus porosus*, of approximately the same length. Among the contrasts with *Crocodylus porosus*, *Baru* possesses deeper jaws with correspondingly exaggerated festoons, more anteriorly situated external nares, a conspicuous jugal crest and posteriorly slanted pseudoheterodont teeth. These features reflect significant differences in the manner of dispatching, and perhaps in its preference of, prey animals.

Sebecosuchian Ziphodonts. Although clearly eusuchian, *Baru* is compared to sebecosuchian crocodiles because of its convergent ziphodont features. With the exception of its laterally compressed, serrated dentition, *Sebecus* shows few

similarities with *Baru*. This is of some importance because the concept of ziphodonty is often broadened to imply a specialised terrestrial predatory complex. The laterally directed orbits, high, narrow, convex snout profile and modifica-

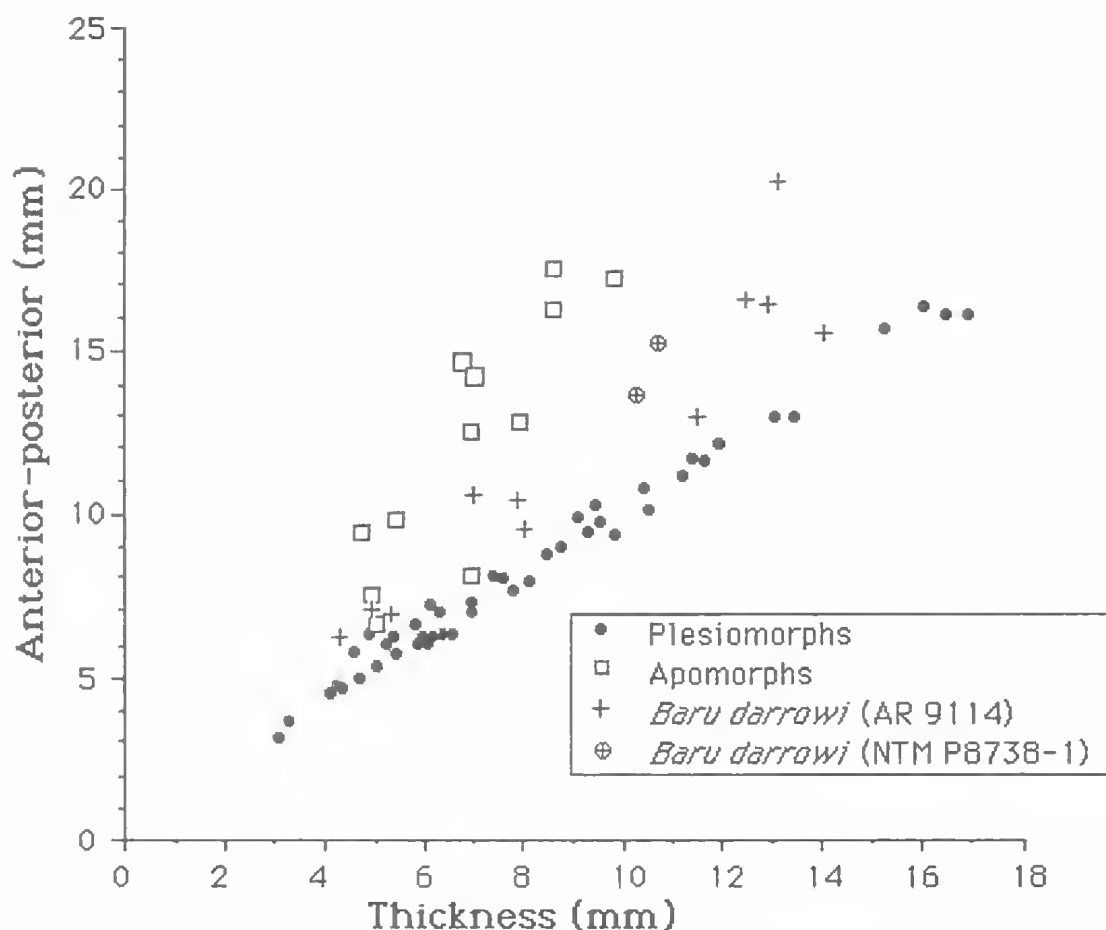


FIG 7. Scatter diagram showing tooth compression in various crocodilians. This shows the teeth of *Baru darrowi* to be more compressed than those of *Crocodylus porosus* and *Alligator mississippiensis* but not as compressed as in the ziphodont forms *Pristichampsus rollinoti*, *Sebecus icaeorhinus* and *Sebecus* sp. Measurements for ziphodont forms from Langston (1956). Measurements for *C. porosus* and *A. mississippiensis* from unnumbered specimens in the Australian Museum reptile collection.

tions of the trochlear surface of the quadrate in relation to specialised jaw mechanics (Colbert, 1946; Langston, 1973) suggest that *Sebecus* was an active predaceous carnivore capable of pursuing prey on land. Although the depth of *Baru*'s snout appears to most closely approach that of *Sebecus* (Table 1) this is a somewhat misleading comparison because the convention of measuring the depth of the snout at the level of the fifth tooth includes the marked alveolar festoon. The proportions of the snouts of the two forms are actually very different; that of *Sebecus* is high and narrow and virtually triangular in section. *Baru*'s snout has a broad-based trapezoidal cross-section and is short and broad. Its lateral profile is strongly concave as opposed to the

convex, narrow bridge of *Sebecus*. More importantly, however, is the typical crocodyline dorsal orientation of *Baru*'s orbits and its nares being sufficiently elevated, despite their terminal position, to allow the head to lie cryptically submerged.

Pristichampsine Ziphodonts. *Baru darrowi* shows a greater degree of overall similarity with the early Tertiary Eurasian eusuchian ziphodonts of the subfamily Pristichampsinae than to the sebecosuchians. However, Pristichampsine crocodiles, known from several species of the genus *Pristichampsus*, are strikingly convergent with the sebecosuchians, not only in their possession of double-serrated and compressed teeth, but in the lateral position of the orbits, the narrow

snout and the similarly specialised craniomandibular joint (Langston, 1973). Although the trochlear surface of *Baru*'s quadrate is imperfectly known, the shape of the quadratojugal and the distal surface immediately preceding the jaw joint are more reminiscent of *Pristichampsus* than *Crocodylus*. The articular of *Baru* indicates that its craniomandibular joint could be modified along the lines of the sebecosuchian and pristichampsine ziphodonts. *Pristichampsus* has a vaulted palate and the skull is narrow, as opposed to broad, across the base of the jugals and through the orbital region. The primary resemblance between *Baru* and *Pristichampsus* is in the lateral view of the snout where the dorsal outline is deeply concave, although the premaxilla of *Pristichampsus* is less bulbous. The teeth are moderately differentiated, at least in some species of *Pristichampsus*, closely approximated and are directed slightly backwards from the maxillary festoon (see Langston, 1973, fig. 4d). The notch for the fourth dentary tooth is weakly developed, particularly when viewed from below and the dentition is considerably less robust than in *Baru*. The teeth of *Baru* are moderately compressed, not as compressed as in the ziphodont crocodilians (i.e. *Pristichampsus* and *Sebecus*) but more so than in less derived crocodilians (Fig. 7).

The palatal morphology of *Pristichampsus* differs from that of *Baru* in possessing well-developed anterior palatine processes, proportionately similar to those of *Crocodylus*. The anterior palatine processes persist among the living short-snouted crocodylids and therefore their presence or absence does not appear to be conditioned by the relative anteroposterior length of the palatal fenestrae. Apparently the resemblances between *Baru* and *Pristichampsus* are largely plesiomorphic for crocodylids but include some elements of the ziphodont trophic complex.

Australasian Endemic Crocodilians. The two endemic *Crocodylus* species, *C. johnsoni* and *C. novaeguineae* are subsumed under the remarks previously made for *Crocodylus*. Besides the formally described endemically Australian genera, *Pallimnarchus* and *Quinkana*, there are other extinct species that are too poorly represented to merit systematic designation. The apparent distinction of the Australian *Crocodylus* species and the remaining known Australian genera makes it improbable that a direct ancestor-descendant relationship between them will be found on this continent. A compelling alter-

native, therefore, is to consider the possibility of a close relationship among the endemic genera not affiliated with *Crocodylus*.

Quinkana fortirostrum Molnar, 1981, is a highly distinctive crocodilian characterised by a broad, short snout with a deep, convex profile, large anteriorly positioned palatal fenestrae and doubly-serrated laterally compressed teeth showing only moderate differentiation along the tooth row. Its short snout and palatal morphology is unlike that of either sebecosuchian or pristichampsine ziphodonts (Table 1), but its dentition is morphologically similar to members of those groups.

The type specimen, AM F.57844, is a fragment of the snout broken immediately anterior to the orbits, but including the anterior margins of the palatal fenestrae and the anterior palatine suture. In section, the rostrum is trapezoidal, with well developed alveolar processes. Due to the position of the break, Molnar (1981) was able to examine the internal structure of the snout cavity. He observed that 'A high, posteriorly concave partition dorsally bounds the anterior margin of the palatal fenestra. A similar but less developed partition is found in *Crocodylus johnsoni*, *C. novaeguineae* and *C. porosus*, where, however, it is placed well anterior to the margin of the fenestra, and is restricted to the lateral portion of the snout cavity. In *Q. fortirostrum* the maxilla is excavated anterior to this partition, forming lateral chambers that open posteriorly. Above the junction of the palatal processes of the two maxillae rise two thin, nearly vertical flanges, which together form a narrow trough along the floor of the snout cavity' (Molnar, 1981). It is therefore of some importance to note that a similar arrangement occurs in *Baru*. However, as this condition is regarded only in contrast to the typical *Crocodylus* condition, we are unsure of the morphology of the same region in other short snouted crocodylids such as *Osteolaemus* and *Paleosuchus* in which the more anterior position of the palatal fenestrae might also determine similar relations. Although described by Iordansky (1973), he does not compare this region in various genera. *Quinkana* and *Baru* lack the anterior palatine processes, which is unusual among crocodilians and apparently not conditioned by the anterior disposition of the palatal fenestrae, or by the proportions of the interfenestral laminae of the palatines. *Quinkana* is otherwise very different from *Baru*, but has few specific similarities with any other group of crocodilians. Thus *Quinkana* has a combination

of characters; some ziphodont features (implying a terrestrial or semi-terrestrial predaceous existence) others unique and a few, very specific and rather compelling features, suggestive of a close relationship with *Baru*.

To date, specimens of *Pallimnarchus pollens* have been fragments and no complete skulls are known (Molnar, 1982). However, nearly complete snouts referable to *Pallimnarchus* have recently become available for study (Willis and Molnar, in prep.). This more complete material reveals that *Pallimnarchus* has anteriorly located palatal fenestrae (anterior level with the seventh alveoli) and lack anterior palatine processes. Teeth referred to *Pallimnarchus* (Molnar, 1982) are distinguished by serrate carinae on a broadly conical form. A more complete comparison with *Baru* will have to wait until the new *Pallimnarchus* material is properly described.

We are unable to fully support the hypothesis that the three known Australian endemic crocodiles represent a monophyletic group because of limited comparative material and incomplete fossils. There is, however, sufficient evidence to indicate that this is a solid alternative to the notion of sebecosuchian and/or pristichampsine ancestry of the group. The possible relationship between these forms are considered in the following section.

CHARACTER ANALYSIS

The following examination of crocodilian character states is based on Molnar (1981), Norell (1989) and Benton and Clark (1988). Molnar used character frequency to determine character polarities where as Benton and Clark, and Norell, used the outgroup method proposed by Maddison et al. (1984). We have accepted the polarity of characters as determined by Molnar, Benton and Clark, and Norell. The polarity of new characters introduced into this study have been determined by their distribution among the ten taxa indicated in Table 3.

SUBORDINAL CHARACTERS

1) Procoelous vertebrae have been found with specimens attributed to *B. darrowi*. No amphicoelous vertebrae are known from deposits from which *B. darrowi* has been found. It is therefore a reasonable assumption that *Baru* had procoelous vertebrae, which is recognised as a eusuchian character (Steel, 1973; Kuhn, 1968). Benton and Clark (1988) recognise procoelous vertebrae as an apomorphy of a group that in-

cludes Eusuchia and an undescribed early Cretaceous crocodile from North America.

2) The movement of the internal nares posteriorly in advanced crocodiles was recognised by Huxley (1875). The internal nares are completely surrounded by the pterygoids in *Baru*. This is regarded as a eusuchian character state (Steel, 1973; Kuhn, 1968; Benton and Clark, 1988).

SUBFAMILIAL CHARACTERS

3) The pattern of tooth enlargement in the crocodilian skull has been used to distinguish members of the Alligatorinae from the Crocodylinae (e.g. Steel, 1973). In alligatorines the fourth maxillary tooth is usually the largest; in crocodylines it is the fifth. In *Baru* the fifth tooth is largest.

4) The presence of a notch between the premaxilla and maxilla can be used to distinguish alligatorines from other crocodilians (Steel, 1973). In crocodilians the fourth dentary tooth fits into this notch when the jaws are closed. In alligatorines this tooth usually fits into a pit in the palate medial to the upper tooth row. *Baru* conforms to the plesiomorphic condition.

5) In *Alligator* and many fossil alligatorines the lacrymal is separated from the nasal bone by the maxilla (a derived condition), whereas in crocodylines and the caimanoid alligatorines the lacrymal contacts the nasals. This may also be expressed as the prefrontals lacking any contact with the maxilla in crocodylines. *Baru* is crocodyline in this respect.

FEATURES OF AUSTRALIAN FORMS

6) *Baru*, *Quinkana* and *Pallimnarchus* have large anteriorly placed palatal fenestrae. This condition appears to be part of a functional complex related to short, broad snouts.

7) Most crocodiles possess an anterior palatine process. *Baru*, *Quinkana* and *Pallimnarchus* lack this process. The only other eusuchian crocodiles for which descriptions are available that lack these structures are those of the American Eocene genus *Brachyuranochampsia*. This is a moderately narrow snouted form with more posteriorly situated palatal fenestrae. Therefore it appears that the lack of the anterior palatine processes is independent of the position of the palatal fenestrae.

8) Molnar (1981) determined interlocking teeth to be a derived crocodilian state. However, Norell (1989) determined that an overbite, as seen in *Baru* and *Quinkana*, is the derived state.

Norell's determination is accepted here because of his use of the outgroup method of Maddison et al. (1984).

9) The conspicuous jugal ridge observed in *Baru* appears to be a unique feature among crocodiles. Its presence in *Baru* is taken to be autapomorphic.

ZIPHODONT CHARACTERS

10) Molnar (1981) considers highly differentiated crocodyline dentitions to be plesiomorphic and more uniform dentitions of longirostrine and ziphodont crocodiles to be derived.

11) Festooning is a plesiomorphic feature. The derived condition is a straight tooth row (Molnar, 1981). These conditions are clearly associated with the degree of size differentiation of the dentition.

12) Extremely narrow snouted eusuchians are derived. Moderately narrow to moderately broad snouts are plesiomorphic. Extremely broad, short snouts are also derived (Molnar, 1981). *Quinkana* and *Baru* are unusual ziphodonts in having short, broad snouts. *Peirosaurus* (Gasparini, 1982) appears to be a ziphodont with a moderately broad or broad snout.

13) According to Molnar's classification, ziphodont crocodilians have deep to moderately deep snouts. He proposes that this is a derived state. Both *Baru* and *Quinkana* have moderately deep snouts. The plesiomorphic condition is a low snout form.

14) Laterally compressed teeth are considered to be derived. The plesiomorphic condition is a tooth of circular or broadly oval cross section. The teeth of *Quinkana* are decidedly compressed whereas those of *Baru* retain the plesiomorphic conical shape towards the base, becoming progressively flattened on the lingual side towards the tip of the crown.

15) Serrations are not known to occur on any round conical crocodilian teeth (with the exception of some teeth attributed to *Pallimnarchus*, Molnar, 1982), they are invariably associated with some degree of transverse compression of the crown. Laterally compressed teeth with serrated edges are termed ziphodont. The ziphodont condition is a derived character state.

16) Posterior inclination of the teeth appears to be an unusual feature in crocodilians. The condition may be present in the sebecosuchian *Baurusuchus* and perhaps to some extent in *Pristichampsus*. The condition is probably a derived one.

DISCUSSION

The most complete cladistic analysis of the Crocodylia is that of Benton and Clark (1988). They left the crocodylids (including gavials, alligators and crocodylines) as an unresolved crown group. Norell (1989) analysed this crown group based on twelve characters and defined the relationship between the gavialinae, crocodylids and alligatorids. Unfortunately, Norell's work was published after this paper had been reviewed and his characters have not been fully incorporated in this analysis. However, *Baru* has all three apomorphies that Norell has used to separate crocodylids from gavials and alligators.

Baru retains many plesiomorphic crocodyline features. Its principle derivations are related to a specialised trophic complex which involves some elements of the so-called ziphodont condition. As is often the case with ancient surviving groups, they are exceptionally conservative in their basic morphology and many lineages have paralleled and converged in their trophic mechanisms. It is under these circumstances that the phylogenetic methodology becomes severely strained. Most apomorphic features are dedicated to trophic adaptations and the field of relevant character states (discrete or exclusive characters independent of functional requirements) are few and difficult to substantiate. In terms of phylogenetics, therefore, we are confined to a single possible synapomorphy, the absence of the anterior palatine process, in uniting the three extinct Australian genera under consideration. Ziphodont teeth have evolved convergently and in parallel, and anteriorly placed palatal fenestrae have evolved independently in the caiman and *Osteolaemus*. We are unable to verify the uniqueness of the similarity of the internal rostral partitioning in *Baru* and *Quinkana* at this time due to lack of the necessary specimens. The absence of the anterior palatine processes appears to be the least trophically related apomorphic character uniting *Baru*, *Quinkana* and *Pallimnarchus* with another group (e.g. *Brachyuranochampsus*). We consider this possible relationship to be a more parsimonious one than basing a relationship with the *Pristichampsinae*, on the assumption that the anterior palatine process was lost in parallel.

The ingroup interrelationship of *Baru*, *Pallimnarchus* and *Quinkana* are little closer to resolution. *Baru* and *Pallimnarchus* are more plesiomorphic than *Quinkana* according to the character polarities used here. However, *Pallimnarchus* is not sufficiently well known to deter-

mine its phyletic position relative to *Baru*. It appears, however, that *Baru darrowi* is too specialised to have given rise to *Quinkana*. We are therefore unable to build a connected sequence and must assume that another clade for which we have no information is involved.

PALAEOBIOLOGY

A detailed functional analysis of *Baru*'s cranial anatomy must preclude any definite conclusions as to the nature of its trophic specialisations. However, its distinctive dentition and robust proportions justify some speculation on the nature of its habits.

The prominent upper and lower festoons bearing large, posteriorly-directed and closely spaced teeth constitute a specialised cleaver-like biting mechanism, designed to deliver an immediate incapacitating blow to its prey. The upper and lower festoons and their dentitions complement one another so as to produce a fulcrum above which the lower caniniforms drive into the prey. The resultant is a combined shearing and tissue deforming (tearing and breaking) action capable of breaching tough, flexible material (thick hides, as well as more durable materials such as armoured skin and perhaps bony carapaces). Because of the fulcrum-like structure of the interposed maxillary festoon, tissues are stretched against and severely deformed by a triangle of forces. The large posteriorly-angled teeth restrain the prey-object during the early phases of jaw closure, when resultant forces exerted by the jaw tend to drive the object forward.

The purpose of the serrations in *Baru* appears to be a secondary refinement in which the struggling movements of the prey combined with small movements of the jaws and perhaps equally importantly, elevation and depression of the head at the craniocervical joint can continue to sever tissues in the grasping period during which the adducted jaws are restricted in their movement.

Baru's dental specialisations are therefore interpreted as a mechanism for rapid immobilisation of relatively large prey. Judging from the dimensions of the type, *Baru* was capable of killing animals up to 300 kg in weight based on analogous feats by the saltwater crocodile. *Baru* would therefore have been a likely predator of mammals and other large crocodiles, as its dental complex and powerful adductor mass was capable of breaching armoured hides.

The remains of *Baru* are consistently associated with fluvio-lacustrine sediments. Its short, broad heavy cranium and the morphology of its atlas-axis complex indicate that it had no greater head mobility than *C. porosus*, which would have limited an active terrestrial predator. Unlike sebecosuchians, pristichampsines and Australia's ziphodont *Quinkana*, *Baru* has dorsally oriented orbits like aquatic crocodiles which spend the majority of their lives partially submerged. We conclude that *Baru* was an aquatic crocodile adapted to shallow, inland freshwater lakes and small streams in which the saltwater crocodile habit of dragging its larger prey into deep water may not have been possible. In shallow water and narrow streams the prey has an opportunity to continue to struggle, whereas the saltwater crocodile is often able to release its half-drowned prey to effect a new grasp. *Baru* probably ambushed large mammals from the edge of streams and shallow lakes relying on its powerful bite to incapacitate its prey through shock-inducing trauma. If *Baru* were a terrestrial or semi-terrestrial form, the risky and energy-consuming action of immediately immobilising its prey would be unnecessary. Large terrestrial reptiles, best known from the studies of the Komodo Dragon by Auffenberg (1982), initially injure large prey by hamstringing it from behind, then follow it until it expires from exhaustion and bleeding. This pattern appears more appropriate to species of *Pristichampsus* and *Quinkana*.

The postulated predatory behaviour of *Baru* is too specialised to suggest a preadaptation to terrestriality for *Quinkana*. However, terrestrial predation in crocodiles probably had its roots in behaviour in which prey was ambushed from the water, then followed onto the land.

CONCLUSIONS

Functional complexes reflecting trophic adaptations, superimposed on a general morphological conservatism have produced numerous convergences within the Crocodylia. Consequently, taxonomic relationships are difficult to unravel.

The contribution of the pterygoids to the secondary palate, posterior intra-ptyerygoid position of the internal nares, confluent external nares, subdermal postorbital bar, small superior temporal fenestra, well developed mandibular fenestra and associated procoelous, keeled cervical vertebrae (NTM P9778) place *Baru* in the Eusuchia, Family Crocodylidae (sensu Romer,

1956). The diagnostic enlarged fifth maxillary tooth and the lateral notch at the maxillo-premaxillary suture to accommodate the fourth mandibular tooth align *Baru* with the Crocodylinae.

Baru shares a number of character states with two other Australian endemic fossil genera. Its incipient ziphodonty, broad snout, presence of a similar arrangement of the internal partition of the maxilla and similar palatal proportions may support a phylogenetic relationship with *Quinkana* and *Pallimnarchus*. The absence of the anterior palatine process in all three of these genera may link them to the Eocene North American taxon *Brachyuranochampsus*, and distinguishes the Australian crocodiles from the pristichampsine ziphodonts.

In *Baru*, the shorter, wider and deeper rostrum, hypertrophied festooning, greatly differentiated tooth size and laterally compressed serrated teeth are a functionally related complex and as such are not reliable taxonomic indicators. Ziphodont teeth have evolved independently in several crocodilian lineages and have been associated with highly specialised, perhaps terrestrial predatory habits. Adaptations apparently suited to a terrestrial predatory mode include a convex deep, dorsal snout profile and dorsolaterally directed orbits and external nares. In contrast, *Baru* has elevated premaxillae, high anterodorsal placement of the external nares, concave dorsal snout profile and dorsally oriented orbits. These features indicate that *Baru* was an aquatic crocodile.

ACKNOWLEDGMENTS

We would like to thank M. Archer, R. Molnar, R. Sadlier and N. Pledge for access to material used in this paper. Ralph Molnar, Sue Hand, John Scanlan and M. Archer provided advice and help in technical matters associated with this paper and assisted with constructive comments on early drafts. Thanks are also extended to Paul Darrow and The Blake's Seven Society of Australia (and in particular Elaine Clark) and Dr Tony Wicken for financially assisting this work. Janine Willis and Heather Bender helped type the final draft.

General support for the Riversleigh Project which enabled some of the material studied here to be obtained was provided by: The Australian Research Grant Scheme (Grant PG A3 851506P); The National Estates Grants Scheme (Queensland); The Department of Arts, Sport,

the Environment, Tourism and Territories; Wang Australia Pty Ltd; I.C.I. Australia Pty Ltd; the Queensland Museum; the Australian Museum; the Australian Geographic Society; Mount Isa Mines Pty Ltd; the Royal Australian Air Force; the Australian Defence Force; the Riversleigh Consortium (Riversleigh being a privately owned station); the Mount Isa Shire; the Riversleigh Society; the Friends of Riversleigh; Probe and the many volunteer workers and colleagues. A Northern Territory Heritage Grant provided funds for documentation of the Camfield Locality. We thank Wayne Brown, Karl Roth and Ian Archibald for their help in excavation.

LITERATURE CITED

- ARCHER, M., GODTHELP, H., HAND, S.J. AND MEGIRIAN, D. 1989. Fossil mammals of Riversleigh, northwestern Queensland: Preliminary overview of biostratigraphy, correlation and environmental change. *Aust. Zool.* 25 (2): 29-65.
- AUFFENBERG, W. 1982. 'The behavioral ecology of the Komodo Dragon'. (University Press of Florida: Gainesville, Florida).
- BENTON, M.J. AND CLARK, J.M. 1988. Archosaur phylogeny and the relationships of the Crocodilia. pp 295-338. *In* Benton, M. J. (ed.), 'The phylogeny and classification of the tetrapods. Vol. 1: Amphibians, reptiles, birds'. Systematics Association Special Volume No. 35A. (Clarendon Press: Oxford).
- COLBERT, E.H. 1946. *Sebecus*, representatives of a peculiar suborder of fossil Crocodilia from Patagonia. *Bull. Amer. Mus. Nat. Hist.* 87: 217-270.
- GASPARINI, Z. 1982. Una nueva familia de crocodrilos zifodontes Cretácicos de America del sur. Quinto Congreso Latinoamericano de Geología Argentina 4: 317-329.
- GROGER-WURM, H.M. 1973. 'Australian aboriginal bark paintings and their mythological interpretation'. (ASIS: Canberra).
- HECHT, M.K. AND ARCHER, M. 1977. Presence of xiphodont crocodilians in the Tertiary and Pleistocene of Australia. *Alcheringa* 1: 383-385.
- HUXLEY, T.H. 1875. On *Stagonolepis robertsoni*, and the evolution of the Crocodilia. *Quart. J. Geol. Soc. London* 31: 423-438.
- IORJANSKY, N.N. 1973. The skull of the Crocodilia. pp.201-262. *In* Gans, C. and Parsons, T.S. (eds), 'Biology of the Reptilia. 4. Morphology D.' (Academic Press: London),

- KUHN, O. 1968. 'Die Vorzeitlichen Krokodile.' (Oeben: Munich).
- LANGSTON, W. 1956. The Sebecosuchia; cosmopolitan crocodiles? Amer. J. Sci. 254: 605-614.
1973. The crocodilian skull in historical perspective. pp. 263-284. In Gans, C. and Parsons, T.S. (eds), 'Biology of the Reptilia. 4. Morphology D.' (Academic Press: London).
1975. Ziphodont Crocodilia. Fieldiana, Geol. 33: 291-314.
- LONGMAN, H.A. 1925. A crocodilian fossil from Lansdowne Station, Mem. Qd Mus. 8: 103-8.
- MADDISON, W.P., DONOGHUE, M.J. AND MADDISON, D.R. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83-103.
- MOLNAR, R.E. 1981. Pleistocene ziphodont crocodilians of Queensland, Rec. Aust. Mus. 33: 803-834.
1982. *Pallimnarchus* and other Cenozoic crocodiles of Queensland. Mem. Qd Mus. 20: 657-673.
- MOOK, C.C. 1921. Skull characters of recent Crocodilia with notes on the affinities of the recent genera. Bull. Amer. Mus. Nat. Hist. 44: 123-268.
- NORELL, M.A. 1989. The higher level relationships of the extant crocodilia. J. Herp. 23 (4): 325-335.
- PLANE, M. AND GATEHOUSE, C.G. 1968. A new vertebrate fauna from the Tertiary of northern Australia. Aust. J. Sci. 30: 272-273.
- ROMER, A.S. 1956. 'Osteology of the reptiles'. (Uni. Chicago Press: Chicago).
- STEEL, R. 1973. Crocodylia. In Kuhn, O. (ed.), 'Handbuch der Palaoherpetologie, Encyclopedia of Paleoherpertology.' Vol. 16. 116 pp. (Gustav Fisher Verlag: Stuttgart).
- TEDFORD, R.H. 1970. Principles and practices of mammalian geochronology in North America. Proc. N. Amer. Paleon. Conv., Sept., 1969: 666-703.
- WEBB, G. AND MESSEL, H. 1978. Morphometric analysis of *Crocodylus porosus* from the north coast of Arnhem Land, northern Australia. Aust. J. Zool. 26: 1-27.
- ZANGERL, R. 1944. *Brachyuranochampsia eversolei*, gen. et sp. nov., a new crocodilian from the Washakie Eocene of Wyoming. Ann. Carn. Mus. 30: 77-84.